

A NOTEWORTHY GILL-LESS HOLOHEPATIC NUDIBRANCH,
OKADAIA ELEGANS BABA, WITH REFERENCE TO
ITS INTERNAL ANATOMY

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FOUR TEXTFIGURES AND THREE PLATES

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I INTRODUCTION

The gill-less holohepatic Nudibranch, *Okadaia elegans* Baba, which forms the subject of this paper was provisionally reported by me in August of last year (1930), adding that it will be necessary to create a new family for this animal. Since then I have been favoured with a good opportunity for carrying on further studies upon the internal organization of *Okadaia*, and am convinced of the necessity for the establishment of a new family, Okadaiidae, to which the following lines

of diagnostic description refer. At the same time I am going to propose here a very interesting morphological fact that in *Okadaia* the suppression of the ctendium is accompanied by the entire disappearance of the circulatory apparatus, a fact never reported before in the Nudibranchiata.

The material upon which the present description is based was collected at Sunosaki and Tateyama, Chiba Pref.; Enosima and Zusi, Kanagawa Pref. It was treated either in the living state under the microscope or in Bouin's solution. Serial sections were cut 7-12 μ thick and stained with Delafield's hematoxylin and eosine.

Before proceeding further, I take this opportunity of expressing my warmest gratitude to Dr. Naohide Yatsu for giving me access to the important literature presented by the late Sir Charles Eliot to the library of the Zoological Institute, Tokyo Imperial University. My hearty thanks are due to Dr. Yaichiro Okada, to whom the generic name *Okadaia* was dedicated, for valuable suggestions and criticisms. Also I must thank Dr. Nils Hj. Odhner who kindly helped me with some of his papers, especially with that which refers to *Heterodoris*.

II DESCRIPTION OF THE OKADAIIDAE, NOV. FAM.

Okadaiidae, nov. fam.

A holohepatic family. Form slender, doridiform. Dorsal surface smooth. Rhinophores finger-shaped, not perfoliated, without vaginae. Branchiae completely wanting on the back. No oral tentacles. Anus and nephroproct situated very slightly to the right of the median line, behind the renal heart. Heart (=true heart), pericardium and vessels entirely absent; the reno-coelomic canal (=reno-pericardial canal) only remains. Renal sac simple, its anterior portion developed into the rhythmically pulsating renal heart. Ureter accompanied by the accessory renal gland. Jaws absent. Radula narrow, ∞ . O. ∞ : no central teeth, laterals few (3 on each side). Liver not ramified but divided into (4) separate lobes opening respectively into the stomach. Hermaphrodite glands consist of (2-3) testes and (5-6) ovaries. Vagina with spermatocyst in addition to the spermatotheca. Vas deferens armed with spines.

In a previous paper (Baba 1930, pp. 47-50), I was very doubtful as to the nature of the heart and the kidney though these names were employed to represent the pulsating chambers and the gland which communicates with the exterior. Further study with special reference to these subjects proved that the preceding names were, as far as comparative histology is concerned, wrongly employed. Consequently the heart and the kidney which appeared in my previous paper are called here the renal heart and the accessory renal gland respectively.

Hitherto the family contained only the type genus

Okadaia Baba, 1930.

Okadaia Baba, 1930 (August), Studies on Japanese Nudibranchs. Venus. Vol. 2, No. 2, pp. 47-48.

At the present time the generic characters are the same as those given above. One species belongs to this genus.

III DESCRIPTIONS OF OKADAIA ELEGANS BABA

Okadaia elegans Baba, 1930

(Textfigs. 1-4; Pl. 5, figs. 1-4; Pl. 6; figs. 1-3; Pl. 7, figs. 1-15.)

Okadaia elegans Baba, l.c. pp. 48-50; Pl. 2, figs. 11-14.

1. Habitat.

The elegant Nudibranch, *Okadaia elegans*, was found underneath stones between tide marks. In Tokyo Bay it reaches maturity and spawns from spring to early summer. The egg-band (Pl. 7, fig. 15), laid on the under surface of a stone, is broad, thin and gelatinous, containing from about eleven to fifteen, large, deep orange-yellow eggs. The life-cycle of this animal is unknown. The known locality is the Pacific coast of Japan (Zusi, Enosima, Tateyama, Sunosaki) where sometimes hundreds of specimens were easily collected. Dr. Okada informs me that the species also occurs in Mutu Bay.

2 External Morphology

The body of *Okadaia elegans* (Pl. 6, figs. 1a, 1b) is slender when wholly extended and crawling on the under surface of a stone. In the preserving fluid the body is much contracted, presenting an almost

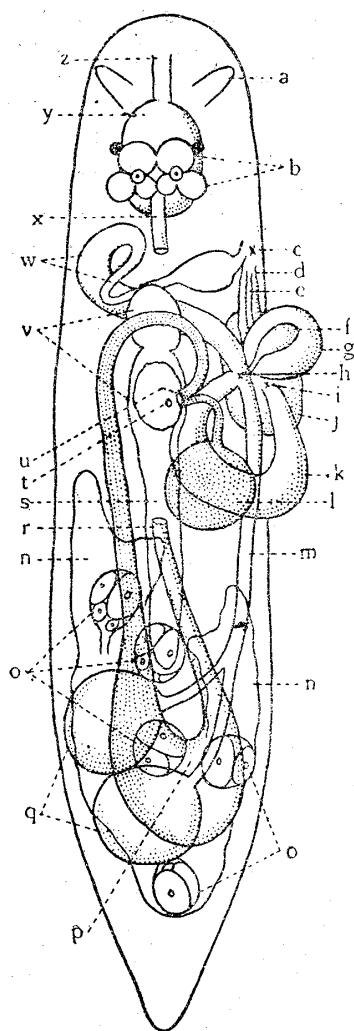


Fig 1.—Dorsal aspect showing arrangement of the visceral organs in the living state; accessory genital glands are removed on the right side ($\times 40$). *a* rhinophore, *b* central nervous system, *c* genital opening, *d* oviduct, *e* vagina, *f* spermatocyst, *g* spermatotheca, *h* hermaphrodite duct communicating with the beginning of the albumen gland, *i* terminal portion of the albumen gland entering the mucous gland, *j* mucous gland, *k* albumen gland, *l* anal organ, *m* hermaphrodite duct, *n* liver lobes, *o* ovaries, *p* stomach, *q* testes, *r* posterior portion of the oesophagus, *s* renal sac, *t* accessory renal gland and the nephroproct, *u* intestine opening into the anus, *v* anterior and posterior chambers of the renal heart, *w* vas deferens, *x* anterior portion of the oesophagus (the intermediate portion between *x* and *r* is cut off), *y* buccal mass, *z* stomodaeum.

globular outline. There is no mantle-margin projecting over the foot as in *Argus* etc.; a cross-section of the body is circular with the pedal sole at the ventral side. The head is rounded and provided with a pair of rhinophores. The rhinophores (textfig. 1, *a*) are finger-shaped, not perfoliated, without vaginae and ciliated throughout the surface. The slit-like mouth is on the ventral side of the head. The genital opening (textfig. 1, *c*) is a little posterior to the head on the right side. The anus (textfig. 1, *u*; Pl. 5, figs. 2, *e*; 3, *d*) opens dorsally to the right of the median line. At the left of the anus the renal pore or the nephroproct (textfig. 1, *t*; Pl. 5, figs. 2, *d*; 3, *c*) is found. The tail is tapering. The back is almost smooth and traces of papillae, granules or spicules are nowhere visible. The pedal sole is ciliated throughout the surface.

The general ground colour of the body is orange-yellow. The colour is faintly deeper at the rhinophores. Two deep blue eyes show themselves through

the integument immediately behind the rhinophores. The posterior portion of the back looks greenish or brownish through internal liver lobes. The opaque white testes, deep orange-yellow ovaries and reddish brown anal organ are some of the striking visceral organs showing through the transparent integument. The pigmented cells to which the general ground colour of the body is due are feebly greenish when alive, and filled with orange-yellow granules. The dorsal epithelium consists of unciliated, low (12μ), cubic cells. Under the epithelium is the subepithelial layer and the loose connective tissue which constitutes the greater part of the body wall. Interspersed between the epithelial cells are goblet-shaped mucous gland cells measuring about $27-32 \mu$ in height. Epithelial cells of the ciliated rhinophores are somewhat larger (about 20μ). The pedal epithelium (Pl. 7, fig. 1) is formed of long (about 20μ), cuticulated and ciliated cells, interspersed between which are multicellular mucous glands. These glands are especially large (about 200μ in height) and numerous at the anterior portion of the pedal sole, but decreasing in size (about 80μ) and number towards the posterior portion (Pl. 5, fig. 4).

3 Internal Morphology

a) Digestive System

The mouth is on the ventral side of the head. The stomodaeum (textfig. 1, z; Pl. 5, fig. 4, j) is a short tube lined with ciliated cells and mucous gland cells. The buccal mass (textfig. 1, y; Pl. 7, fig. 10, a) is large (0.3 mm long) and has an odontophore loaded with the radula. The inner wall of the buccal mass is thickly chitinized at the anterior portion; jaw-plates are entirely absent. The radula formula is $35 \times 3.0.3$ (Pl. 7, fig. 5). The innermost tooth is pointed at the apex, the outermost plate-like and the intermediate hamate. The oesophagus (textfigs. 1, x, r; Pl. 5, fig. 4, n; Pl. 7, fig. 10, c) leaves the dorsal side of the buccal bulb, runs under the visceral mass and leads to the stomach (textfigs. 1, p; 2, k; Pl. 5, fig. 4, s). The most anterior

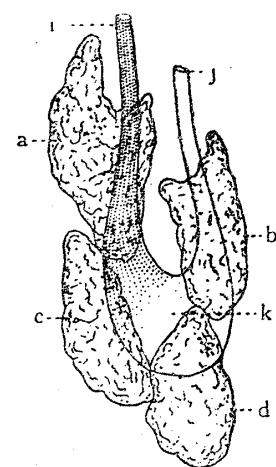


Fig. 2—Dorsal aspect of the stomach with four liver lobes in natural position ($\times 40$). For detailed explanations see under textfig. 3.

portion of the oesophagus is small, folded internally and lined with ciliated low (12μ) cells, while towards the posterior portion the intestine becomes large and smooth internally. The stomach is a large, thin-walled sac tinged with orange-yellow when alive. In sections the

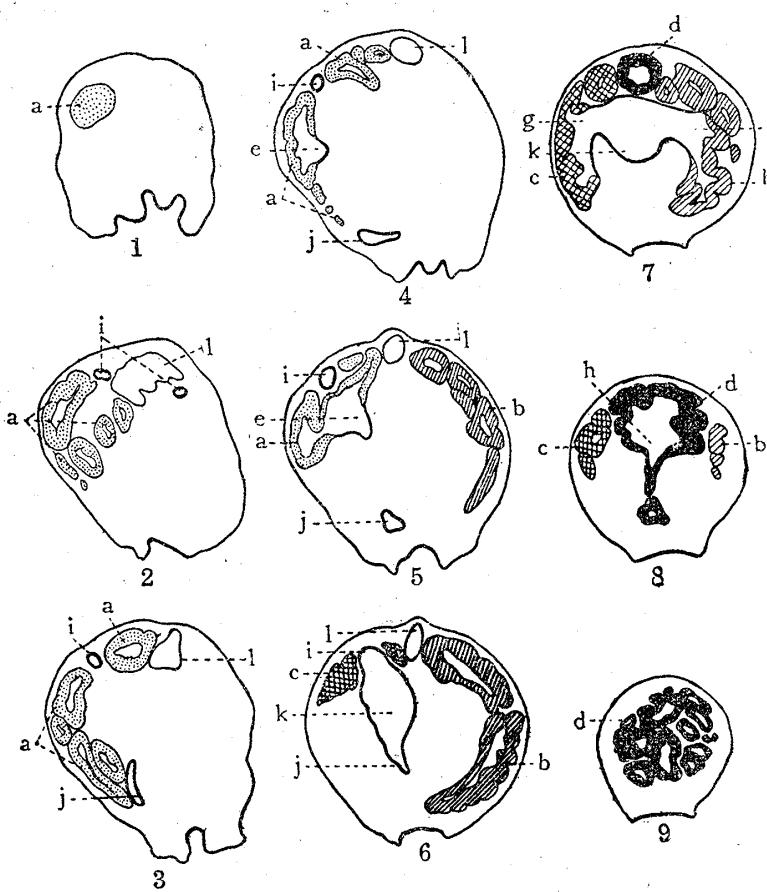


Fig. 3—Transverse section through successive portions (1-9) of the body, showing the relation between the stomach and the four liver lobes. 1 anterior and 9 posterior. Each section is cut 12μ thick and the distance between the successive sections is 132μ ($\times 40$). The following explanations apply to both textfig. 2 and textfig. 3. a anterior left lobe, b anterior right lobe, c posterior left lobe, d posterior right lobe, e opening of the anterior left lobe, f of the anterior right lobe, g of the posterior left lobe, h of the posterior right lobe into the stomach, i intestine, j oesophagus, k stomach, l renal sac.

cavity of the stomach is filled with undeterminable foodstuff which stains with hematoxylin. The stomach is beset with liver masses (textfig. 2). In a fresh condition, the liver is greenish or somewhat brownish, describing a U-shaped half-ring at the dorsal and posterior portion of the haemocoele. But a reconstruction of the liver by serial sections (textfig. 3) shows that this organ is composed of four lobes opening with a wide mouth into the stomach respectively. The anterior left liver lobe (textfigs. 2, a; 3, a; Pl. 6, fig. 3, 1) opens from the left side, the posterior left one (textfigs. 2, c; 3, c) from the left side, the posterior right one (textfigs. 2, d; 3, d; Pl. 5, fig. 4, q) from the dorsal side, and the anterior right one (textfigs. 2, b; 3, b) from the right side into the stomach. The liver is thus divided into four lobes but shows no trace of ramification. The gall-bladder is absent. Microscopically the wall of the liver is formed of a single layer of secretory gland cells (Pl. 7, figs. 2, c; 3, a, b) measuring about 45μ high. The cell contents of the gland cell are granular and stain with eosine. Interspersed between, or detached from the secretory hepatic gland cells, are elliptic or roundish cells (Pl. 7, fig. 2, a) of various sizes ($110 \times 160 \mu$ to $240 \times 300 \mu$). The protoplasmic portion is filled with minute refractive granules which stain feebly with hematoxylin. These cells seem to be the so-called hepatic cells, excretory in function.

The intestine (textfig. 1, u; Pl. 5, fig. 4, h) passes from the dorsal side of the stomach forewards and, after describing a broad loop, opens into the anus. The intestine is orange-yellow when alive. The inner wall of the intestine has several longitudinal folds at the posterior portion. The lining cells (Pl. 7, fig. 6) of the intestine are low (about 8μ) and ciliated. Into the anus opens the internally ciliated duct of the saccular anal organ (textfig. 1, 1; Pl. 5, fig. 3, h; Pl. 6, fig. 2, b, c). This organ measures about 0.2 mm in diameter and, when fresh, is deep reddish brown. It is thin-walled (Pl. 6, fig. 2, b; Pl. 7, fig. 11) with a few, large nuclei which bulge out inwards and measure about $14 \times 16 \mu$. When alive the anal organ is filled with reddish brown granules. These granules stain with hematoxylin in a mounted section.

b) Nervous System

The central nervous system (textfig. 1, b; Pl. 7, fig. 10) lies on

the dorsal side of the oesophagus at its anterior portion and surrounds it. It is composed of four pairs of ganglia, viz. cerebral, pedal, pleural and buccal. Cerebral ganglia are large and are accompanied by black eyes and otocysts containing one otolith each. Buccal ganglia are small and lie on the postero-dorsal side of the buccal mass under the oesophagus.

c) Circulatory and Excretory System

In sections no traces of the proper pulsatory centre or the heart and the pericardium comparable with those in the other Nudibranchs were found.

The haemocytes (Pl. 7, fig. 14, c) are irregular in outline and comparatively large; some of them measure about $11 \times 17 \mu$, $6 \times 16 \mu$, $12 \times 12 \mu$ etc. The cell contents of the haemocyte are minutely granular and stain with eosine. The transparent renal sac (text-fig. 1, s; Pl. 5, figs. 3, a; 4, b), which is the proper excretory organ in the Nudibranchiata, is a long, simple organ lying on the mid-dorsal line in the haemocoele. Histologically the wall of the renal sac (Pl. 7, fig. 14, a) consists of large (about 17μ high), vacuolated, clear, cubic or quadrangular cells. The protoplasmic portion of the renal cell is limited to a small quantity round the nucleus at the base of the cell and stains faintly with eosine.

The anterior prolongation of the renal sac is divided into two rhythmically pulsating chambers (textfig. 1, v; Pl. 5, fig. 3, f), called the renal heart in this paper. Between these two chambers occurs a sacculation like a circular septum. In sections the anterior one of the two chambers is a little smaller than the posterior one. There occurs no clear separation or sacculation between the renal sac proper and the renal heart, but the former goes into the latter, increasing in size.

The two chambers of the renal heart carry on a movement in such a way that the contraction of one chamber follows the enlargement of the other. Such a rhythmic movement of the renal heart recalls to mind the beat of the heart. I mistook the renal heart for the true heart in my previous paper. Histological study shows that the lining cells of the renal heart are of the same nature as those of the renal sac. Hence it may be considered that the renal heart is

nothing but a specialized portion of the renal sac. My reason for employing the name, "renal heart," will be explained in the chapter on General Considerations.

From the postero-lateral side of the posterior chamber of the renal heart, on the right side, a short canal (Pl. 5, figs. 1, f; 3, g; Pl. 7, fig. 12) leaves and is directed obliquely to the ventral side of the haemocoele. The free extremity of the canal is kept in place by the connective tissue. The internal cavity of the renal heart and the renal sac communicates with the haemocoele through the preceding canal. This canal measures about $90\ \mu$ in length, the lining cells of which are about $10\ \mu$ high, and is provided with long ($20\ \mu$) cilia. The cilia are directed from the haemocoele towards the renal heart.

There are no traces of vessels leaving the renal sac and the renal heart except for the ureter which forms a communication between the renal heart and the exterior. The ureter (Pl. 5, figs. 1, e; 2, d) leaves the posterior chamber of the renal heart at a point immediately above the reno-coelomic communication, and after sending a side branch into the accessory renal gland goes directly to the nephroproct (textfig. 1, t; Pl. 5, figs. 2, d; 3, c). The ureter is ciliated internally.

The accessory renal gland (textfig. 1, t; Pl. 5, figs. 1, c; 2, c; 3, b; 4, g) in life is an opaque white compact gland lying on the dorsal side of the renal sac. The duct of this gland is, as is described above, connected with the ureter. From these reasons this gland is called the accessory renal gland. This gland is composed of exceedingly tall (more or less than $60\ \mu$) pyramidal gland cells (Pl. 7, fig. 13) with very fine tips and broad bases where large nuclei ($8\ \mu$ in diameter) lie. It appears to me that the tips of the gland cells are interspersed between ciliated epithelial cells which line the branch of the ureter entering the accessory renal gland. The gland cells are filled, when alive, with opaque white granules which stain with hematoxylin in a mounted section.

The function of the accessory renal gland is not yet determined, but judging from the general aspect it must be a secretory (or excretory?) gland.

d) Reproductive System

The genital glands (textfig. 4) are differentiated into two testes

and five ovaries or sometimes three testes and six ovaries. These glands attain their full development from spring to early summer. When ripe the ovaries which contain one or two full-grown orange-yellow egg-cells show themselves through the transparent skin. The testes (textfigs. 1, q; 4, lie at the left and ventral side of the haemocoele, under the liver lobes. In the living state the testes are opaque white, bearing orange-yellow flecks on their peripheries. The size of the test is about 0.4 to 0.5 mm in diameter. But when three testes are present

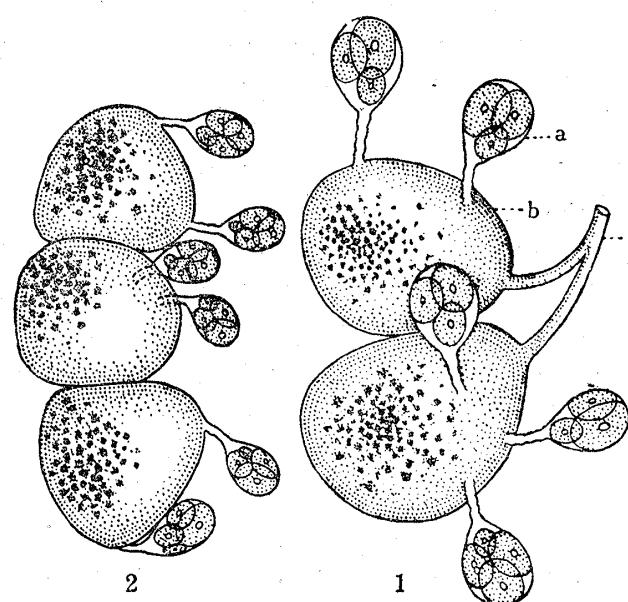


Fig. 4—Relation between testes and ovaries. 1. an individual with two testes (b) and five ovaries (a). c hermaphrodite duct. 2. Another individual with three testes and six ovaries ($\times 60$).

in one individual, they seem to be comparatively small. The wall of the test (Pl. 6, fig. 3, h) consists of several layers of lining cells in which sperms originate. The sperms are produced in groups, fastened together by their heads. The head of the sperm is conical, a little sinuous and stains deeply with hematoxylin, while the tail is strikingly elongated and measures about 200μ in length. The ducts (textfig. 4, c; Pl. 6, fig. 3, g) which leave both of the testes unite immediately

to form one common duct or the hermaphrodite duct, the inner wall of which is ciliated throughout the surface.

The ovaries (textfigs. 1, o; 4, a) develop well from spring to early summer and are about 0.25×0.35 mm in size. Each ovary (Pl. 6, fig. 3, b) contains one or two ripened ova free in the internal cavity. Several egg-cells in various stages of development are attached to the inner wall of the ovary. The ovum is elliptical, about 0.15×0.2 mm or more in size and is filled with granules of a deep orange-yellow colour round the transparent nucleus. Each of the ovaries is attached to the testes with a slender duct (textfig. 4; Pl. 6, fig. 3, i). This duct is thin-walled and is about 170μ long. When there occur two testes in one individual, the anterior bears two and the posterior three ovaries. And in an individual which has three testes, each is accompanied by two ovaries.

The hermaphrodite duct (textfig. 1, m) goes forward along the left side of the oesophagus and is united with the duct of the spermatocyst at the point where the hermaphrodite duct communicates with the beginning of the albumen gland (textfig. 1, h; Pl. 6, fig. 2, p). The vas deferens (textfig. 1, w) swells and then goes into a slender, armed duct, the terminal portion of which swells again and debouches to the exterior. The vas deferens (Pl. 7, fig. 4) is armed with hooks.

The albumen gland (textfig. 1, k; Pl. 6, figs. 2, o, u; 3, d) is a large, curved canal, the wall of which is lined with two sorts of cells (Pl. 7, fig. 7): (1) very large (about 65μ high) secretory cells filled, when alive, with transparent, large granules which stain with eosine in the mounted section; (2) ciliated cells lying between the secretory cells and provided with nuclei near the distal portion. Under low magnification, therefore, the inner wall of the albumen gland appears to be ciliated throughout the surface.

The terminal portion of the albumen gland (textfig. 1, i; Pl. 6, fig. 2, k) is thin-walled (about 20μ thick) and plunges into the cavity of the mucous gland. This portion is distinguished histologically into two successive parts (Pl. 6, fig. 2, l, m; Pl. 7, fig. 9, a, b). The part immediately next to the albumen gland cells is lined with secretory gland cells, the contents of which are minutely granular and stain deeply with eosine in contrast to the albumen gland cells. Ciliated

interstitial cells are interspersed between these secretory gland cells. The wall of the other part which follows the just-mentioned part and continues to the mucous gland consists of secretory gland cells and ciliated interstitial cells. The minutely granular contents of these gland cells stain deeply with hematoxylin.

The mucous gland (textfig. 1, j; Pl. 6, fig. 2, j) is a little smaller than the albumen gland and lies at the ventro-lateral side. The lining gland cells (Pl. 7, fig. 8) are about $40-50\mu$ in height and are filled with granules which stain with hematoxylin. Ciliated interstitial cells are also present here.

A thin-walled oviduct (textfig. 1, d; Pl. 6, fig. 2, h) arises from the anterior portion of the mucous gland and goes to the genital opening. The oviduct is ciliated internally. From the anterior portion of the oviduct the internally ciliated vagina (textfig. 1, e; Pl. 6, fig. 2, i) arises and goes to the spermatotheca (textfig. 1, g). The spermatocyst (textfig. 1, f) is present in addition to the spermatotheca, but the communication between the two organs could not be determined. Both the spermatotheca and spermatocyst are thin-walled and filled with bundles of sperms.

IV GENERAL CONSIDERATIONS

As is described above, the organization of *Okadaia elegans* is very characteristic both externally and internally in the Nudibranchiata. In the general body form *Okadaia* resembles *Acteonia* (= *Cenia*) of the order Sacoglossa, but the presence of the ramified liver and a single row of radula (o.i.o) in the latter genus is the striking difference between the two genera.

Most of the Nudibranchiate molluscs have the secondary branchial apparatus on the dorsal side, mantle or on the lateral side of the body. *Okadaia* has none. In the absence of branchiae the following genera resemble *Okadaia*.

List of gill-less Nudibranchs¹:—
Tribe Holohepatica

¹ With regard to the enumeration of gill-less Nudibranchs I owe much to Eliot and Evans (1908, p. 292-294). *Timorella* (Bergh, Siboga Exped., 1905, p. 241-242) is omitted from the list because the systematic position of this genus is not determined satisfactorily.

Doridoxidae

1 *Doridoxa* Bergh, 1900.

Okadaiidae

2 *Okadaia* Baba, 1930.

Tribe Cladohepatica

Duvauceliidae=Tritoniidae

3 *Tritoniella* Eliot, 1907.

4 *Tritonidoxa* Bergh, 1907.

Notaeolidiidae

5 *Charcotia* Vayssi  re, 1906.

Phylliroiidae

6 *Phylliro  * P  ron and Lesueur, 1810.

7 *Ctilopsis* Andr  , 1906.

8 *Cephalopyge* Hanel, 1905.

9 *Boopsis* Pierantoni, 1923.

Dironidae

10 *Dirona* (MacFarland, 1912), Cockerell and Eliot, 1905.

Pleuroleuridae

11 *Pleuroleura* Bergh, 1874 = *Dermatobranchus* v. Hasselt, 1824.

12 *Heterodoris* (Odhner, 1926) Verrill, 1882.

Doridoeidae

13 *Doridoeides* Eliot and Evans, 1908.

Hedylidae

14 *Hedyle* Bergh, 1895.

Pseudovermidae

15 *Pseudovermis* Kowalevsky, 1901.

We know from the foregoing list that the gill-less forms are uncommon in the Nudibranchiata, especially in the tribe Holohepatica where *Doridoxa* was the only known gill-less Dorid in the past. *Okadaia* is one more gill-less form added to our knowledge.

The simple and unvaginated rhinophores in *Okadaia* must be representatives of the most primitive condition in the Holohepatica. Similar rhinophores are absent in the Holohepatica but present in several genera of the Cladohepatica, namely *Stiliger*, *Ercolania*, *Phylliro  *, *Gonie  lis*, *Calma*, *Hedyle*, *Pseudovermis*, etc.

It appears to me that the position of the anus in *Okadaia* is morphologically important, because it is intermediate between the mid-dorsal anus in most of the Holohepatica and the lateral (right) anus widely found in the Cladohepatica.

The unramified liver in *Okadaia* should be regarded as the holohepatic type, but the divided condition of this organ is aberrant in the Holohepatica. The similarly divided condition of the liver is, on the contrary, recorded in some of the Cladohepatica (e. g. Phylliroidae, Dironidae, *Charcotia*, *Heterodoris*). The Phylliroidae has 3-4, the Dironidae 4 and *Charcotia* as well as *Heterodoris* 3 hepatic lobes. We cannot infer from the preceding facts the systematic relation between *Okadaia* and the cladohepatic Nudibranchs which have divided liver lobes or caeca, because the connection among the holohepatic liver (in the Holohepatica, Duvauceliidae), the divided liver (in the Phylliroidae, Dironidae etc.) and the ramified liver (in most of the Cladohepatica) is not yet cleared up phylogenetically.

As for the function of the anal organ I must confess I am ignorant. In *Janus* the anus is provided with the anal gland (Trinchese, 1881; Pelseneer, 1894; Henneguy, 1925) which is thought to be defensive against enemies by secreting some poisonous matter. But the anal organ of *Okadaia* is histologically far different from the anal gland of *Janus*. The reddish-brown contents were not poured out from the anal organ of *Okadaia* even by pressing the body.

The two rhythmically contracting chambers of the renal heart recall to mind the ventricle and auricle of the heart. But the presence of both the efferent duct (possibly = ureter) and the afferent canal (possibly = reno-pericardial canal) and the absence of vessels show that the renal heart is only a specialized portion of the renal sac. Also the nature of lining cells proves that the renal heart originates in the renal sac. It appears to me that the renal heart in *Okadaia* is somewhat allied to, if not identical with, the "cor renal" or "Nierenspritz" in *Phyllidia*, *Armia* = *Pleurophyllidia*, *Pleuroleura*, *Melibe* etc. where the "cor renal" is situated at the beginning portion of the renopericardial canal, close to the nephrostome. I call here provisionally both of the rhythmic chambers in *Okadaia* the renal heart.

Now the rhythmic movement of the kidney in the Nudibranchiata

is never improbable. Kowalevsky (1901 b, p. 14) shows the case clearly in his description of *Hedyle tyrtowii* Kowalevsky, saying "Il (=le rein)....., et se présente sous la forme d'un grand sac pulsatile qui exécute des contractions rythmiques."

The reno-coelomic canal in *Okadaia* is no doubt homologous with the reno-pericardial canal in *Janus* (Henneguy, 1925), *Hermaea* (Trinchesse, 1877); *Caloria* (Trinchesse, 1888), *Pseudovermis* (Kowalevsky, 1901 a b), etc. and is possibly the simplest form in the Nudibranchiata. According to my opinion, the reno-coelomic canal can be nothing else than the remnant of the reno-pericardial canal which, after losing its communication with the pericardium possibly owing to the degeneration of the latter organ, came to open into the haemocoel. If the pericardium and the heart are really present in *Okadaia*, these organs should be found near the free extremity of the reno-coelomic canal. From the explanation above given, I intend to call the remnant of the reno-pericardial canal in *Okadaia* the reno-coelomic canal.

From a morphological point of view, the lateral (right) and obliquely (dorso-ventral) directed position of the reno-coelomic canal appears to be of much importance, when we come to speculate on the theoretical position of the missing, right ctenidium which, in all of the Nudibranchiata, is in close connection with the pericardium round the heart and, even though indirectly, with the reno-pericardial canal.

The free extremity of the reno-coelomic canal in *Okadaia* opens into the haemocoel and hence it is imaginable that the coelomic fluid or the lympha flows through the strongly ciliated reno-coelomic canal into the renal heart or the renal sac. Also it is not impossible that the haemocytes floating in the coelomic fluid enter the renal heart or the renal sac. But in sections the cavities of the renal heart and the renal sac are empty. I now avoid further speculation on the function of the renal heart and the reno-coelomic canal. The solution of the physiological meaning of these organs must be left to further investigations.

Are there any genera of Nudibranchiate molluscs in which the heart is entirely degenerated? The known gill-less forms as Phylliroidae, *Dirona*, *Pleuroleura*, *Heterodoris*, *Doridoeides* and *Doridoxa* retain heart, pericardium and vessels. *Tritoniella*, *Tritonidoxa*, *Charcotia* and *Timorella* are not thoroughly studied and we cannot state safely the presence or

absence of their hearts. In *Hedyle weberi* Bergh, Bergh (1895) described clearly the presence of the heart and pericardium, while Kowalevsky (1901 b) had difficulty in seeing them in *Hedyle tyrtowii* Kowalevsky. The last-named author (1901 a, b) doubtfully traced the heart in *Pseudovermis paradoxa* Périaslavzeff and clearly in *Hedyle spiculifera* Kowalevsky. From the explanation above given we know *Okadaia* is the only known Nudibranchiate mollusc in which branchiae together with the heart, pericardium and vessels have entirely disappeared.

It is doubtful whether the absence of the blood-gland in *Okadaia* shows one of the important diagnoses of the Cladohepatica. It is true that the Holohepatica have the blood-gland and the Cladohepatica have none, but at the same time we must not forget that the blood-gland is accessory to the circulatory organ, lying at the beginning of the aorta. And it is not impossible, therefore, to consider from a morphological point of view that the disappearance of the blood-gland was caused by the degeneration of the circulatory organs (e. g., heart, pericardium, vessels). In the opaque-white colour and massive appearance the accessory renal gland may be taken for the blood-gland, but the two preceding glands are clearly distinguished histologically from each other (for the sake of comparison I have studied the blood-gland of *Kaloplocamus croceus* Philippi). Yet the morphological and physiological meaning of the accessory renal gland is unknown.

We now proceed further to the consideration of the meaning of the gill-less forms in the phylogeny of the Nudibranchiata. Eliot (1908, p. 295) after his study on *Doridoeides*, said "But the Nudibranchiata are admittedly derived from the Tectibranchiata by suppression of the ctenidium and, as parallel forms are found with and without secondary gills among the less specialized nudibranchs (e. g., *Tritonia* and *Tritonidoxa*), it may be that the gill-less forms remain as a record of the first weak effort to develop a new type which greatly increased in strength and variety by the acquisition of secondary branchiae." "On the other hand if the forms with gills are supposed to be the earlier, it is not obvious why so many families have lost their gills." When this theory is accepted, it will be considered that the ancestors of the Nudibranchiata lost the ctenidium in the past, leaving behind the circulatory system in connection with the newly developing secondary gills, and

that in *Okadaia* the suppression of the ctenidium was accompanied by the entire degeneration of the heart, pericardium, vessels and possibly (?) blood-gland. Hence we have to regard the genus *Okadaia* as one of the most primitive or retrogressive form in the Nudibranchiata.

Eliot (1908, p. 294) pointed out further that the already known gill-less Nudibranchs are not much different in organization from the forms with gills except that the former is less numerous in species and probably in individuals than the latter. But we know from the present study on *Okadaia* that the disappearance of the ctenidium has a great influence over the internal organization, as is shown above. And it is worthy of notice that the gill-less Dorid, *Okadaia elegans*, is, despite the absence of gills and the true heart, strikingly numerous in individuals though it is generally much smaller in size than the gill-bearing Nudibranchs.

The renal sac in *Okadaia* is one of the simplest form in the Nudibranchiata. Similar, saccular renal sacs are known in the Phylliroidae, *Pseudovermis*, *Hedyle* and *Heterodoris*.

The arrangement of the testes and ovaries in *Okadaia* is obviously characteristic among the holohepatic Nudibranchiata.

V CONCLUSION

(1) In the general body form, unramified liver, absence of jaws together with the middle teeth of the radula and the presence of both the spermatotheca and speamatocyst, *Okadaia* belongs to the holohepatic Nudibranchiata.

(2) The simple rhinophores, divided liver lobes and the want of a gall-bladder in *Okadaia* recall to mind the characteristics in the cladohepatic Nudibranchiata. The systematic meaning of the absence of a blood-gland in *Okadaia* is to be questioned.

(3) *Okadaia* differs much from the Doridoxidae which was the only known gill-less form in the holohepatic Nudibranchiata in the dorso-lateral position of the anus, simple rhinophores, radula formula, want of jaws, divided liver lobes, absence of the heart and pericardium and the arrangement of genital glands. *Okadaia*, therefore, must be regarded as a representative of a new family, Okadaidae.

(4) From the disappearance of branchiae and the proper circulatory centre, the Okadaeidae may be considered as the most primitive or retrogressive form in the Holohepatica, while on the other hand the direct connection between the Okadaeidae and other Nudibranchiate families is not yet clear.

(January 20, 1931).

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PLATE 5

Fig. 1. Transverse section of a portion *x* of a contracted specimen (Pl. 5, fig. 4). The section is cut 7 μ thick. This figure shows chiefly the relation between the renal heart and the haemocoele. ($\times 80$). *a* posterior chamber of the renal heart, *b* haemocoele, *c* accessory renal gland, *d* side branch of the ureter entering the accessory renal gland, *e* ureter starting at the renal heart, *f* reno-coelomic canal, the inclination of which is shown by the sagittal mark, *g* theoretical position of the missing pericardium, *h* haemocytes, *i* theoretical position of the missing ctenidium, *j* rhinophore, *k* buccal mass, *l* central nervous system, *m* anterior left liver lobe, *n* anterior chamber of the renal heart, *o* intestine, the outline of which is marked.

Fig. 2. Right half of the transverse section passing a point 21 μ behind the foregoing figure. This section is also 7 μ thick and shows the dorso-lateral openings of the intestine and ureter. ($\times 80$). *a* renal heart, *b* haemocoele, *c* accessory renal gland, *d* opening of the ureter, *e* anus, the outline of the intestine is marked by a sagittal line. Note by the combination of Fig. 1 and Fig. 2 that the ureter starts at the posterior chamber of the renal heart and, after sending a side branch into the accessory renal gland, debouches to the exterior.

Fig. 3. Lateral aspect of the renal heart and the renal sac in the living state. The mark *x* indicates the dorsal side. ($\times 45$). *a* renal sac, *b* accessory renal gland, *c* opening of the ureter, *d* anus, *e* intestine, *f* rhythmically contracting renal heart, *g* reno-coelomic canal, *h* anal organ.

Fig. 4. Mid-dorsal longitudinal section when the body is contracted. ($\times 70$). *a* ovaries, *b* renal sac, *c* albumen gland, *d* communicating duct of the albumen gland with the mucous gland, *e* armed portion of the vas deferens, *f* enlarged, anterior portion of the vas deferens, *g* accessory renal gland, *h* anterior portion of the intestine, *i* central nervous system, *j* stomodaeum, *k* buccal mass, *l* posterior portion of the vas deferens, *m* communication of the hermaphrodite duct with the albumen gland, *n* oesophagus, *o* posterior portion of the hermaphrodite duct, *p* testes, *q* posterior right liver lobe opening into the stomach (*s*), *r* spermatocyst. The digestive tract from the stomodaeum to the intestine is shown by the sagittal line passing *j*, *n* and *s* to *h*. The sperms leave *p* and pass along *o*, *m*, *l*, *e* to *f*, while the eggs pass along *o*, *m*, *c* forward to *d*.

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PLATE 5

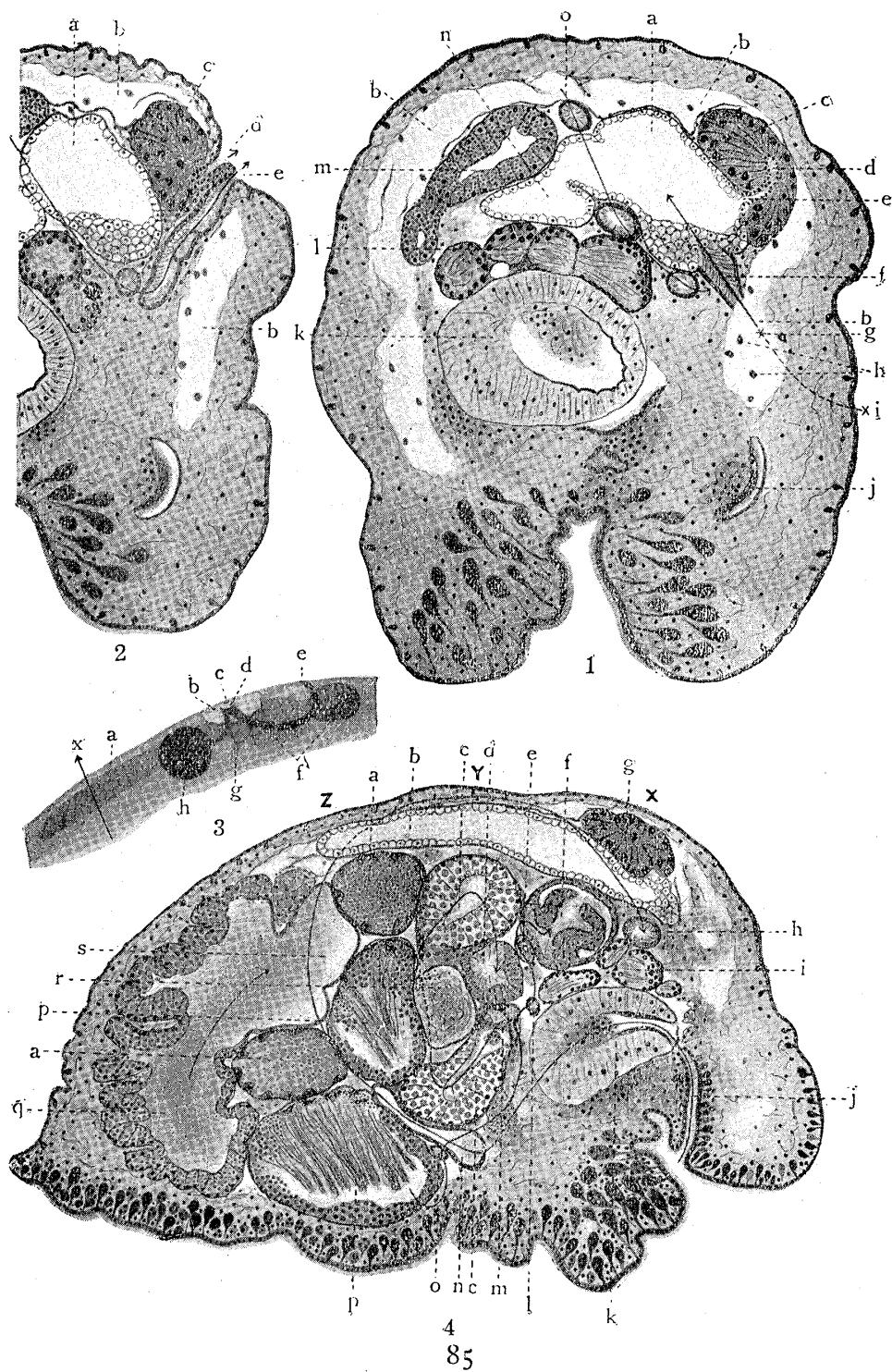


PLATE 6

Fig. 1 a. Dorsal aspect of *Okadaia elegans* in the living state. ($\times 7$).

Fig. 1 b. Ventral aspect of the same specimen. ($\times 7$).

Fig. 2. Transverse section passing through the portion γ of a contracted specimen (Pl. 5, fig. 4). a renal sac, b anal organ, c duct of the anal organ, d anterior portion of the vas deferens, e mucous gland, h oviduct into which the mucous gland (j) opens and from which the vagina (i) starts; the oviduct opens into the female genital opening (g), k portion through which the albumen gland passes to the mucous gland. Here the two successive parts (m and l) are distinguished histologically; m part stains with eosine, l part stains with hematoxylin., n oesophagus, o albumen gland, p communication of the hermaphrodite duct with the albumen gland, q anterior left liver lobe, r testis, s duct of the ovary, t ovary, u albumen gland which connected with the mucous gland, v intestine. The sperms pass from the hermaphrodite duct, along p and d , to the male genital opening (f); the eggs trace p , o , u , k and j to the female genital opening (g). These paths are shown by the sagittal lines. ($\times 80$).

Fig. 3. Transverse section passing the portion z of Pl. 5, fig. 4. ($\times 80$). Note the relation between the testis and ovary. a posterior portion of the renal sac, b ovary, c anterior right liver lobe, d posterior portion of the albumen gland, e mucous gland, f oesophagus, g hermaphrodite duct leaving the testis (h), i communication of the ovary with the testis, j stomach, k anterior left liver lobe with its opening (l) into the stomach, m internally folded posterior portion of the intestine.

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PLATE 6

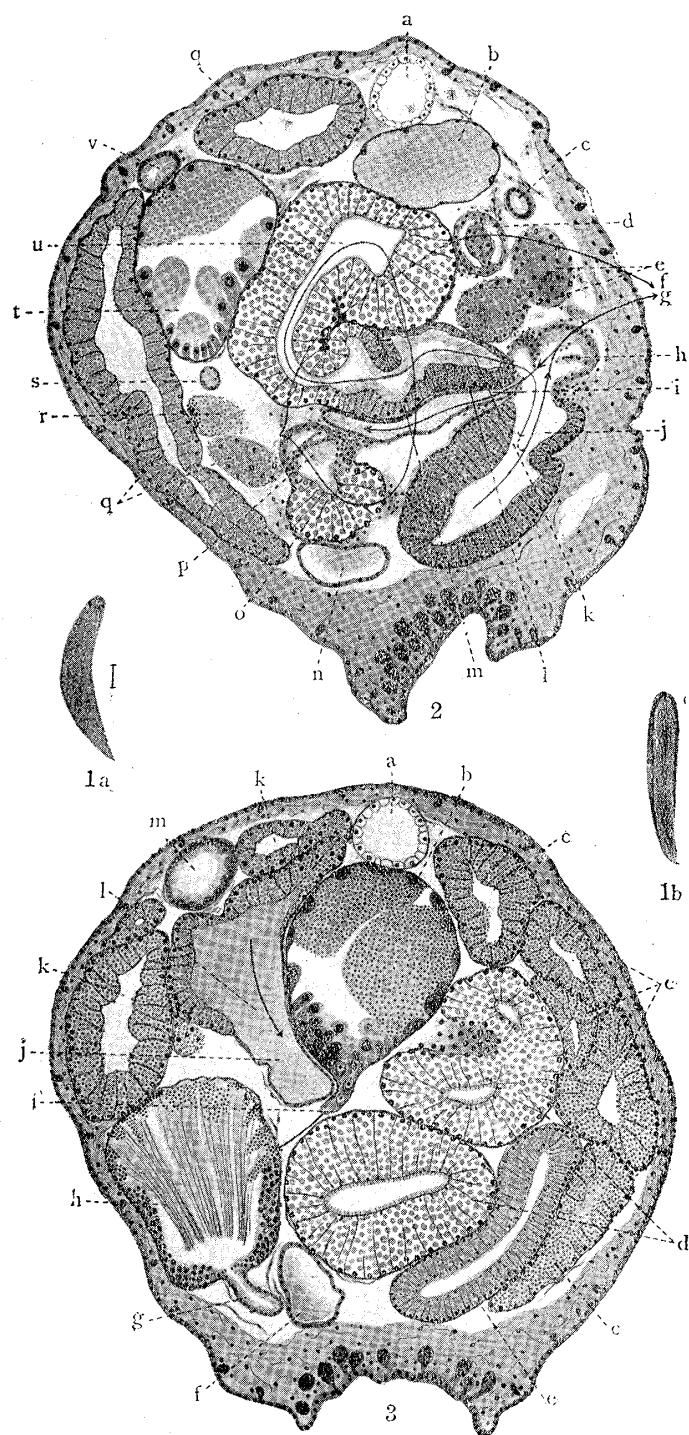


PLATE 7

Fig. 1. Integument of the anterior pedal sole, showing the ciliated epithelium and multicellular mucous glands. ($\times 270$).

Fig. 2. Secretory hepatic cells filled with granules (*c*) and three hepatic cells excretory in function (*a*). *b* peritoneum. ($\times 270$).

Fig. 3. Resting hepatic cells (*b*). *a* cell at the beginning of activity, *c* peritoneum. ($\times 270$).

Fig. 4. Longitudinal section of the armed vas deferens. ($\times 270$).

Fig. 5. Dorsal aspect of the radula. ($\times 400$).

Fig. 6. Inner wall (*a*) of the posterior intestine. *b* peritoneum. ($\times 700$).

Fig. 7. Lining cells of the albumen gland. ($\times 270$). *a* ciliated interstitial cells, secretory gland cells filled with granules, *c* peritoneum.

Fig. 8. Inner wall of the mucous gland. ($\times 270$). *a* interstitial cells, *b* secretory gland cells, *c* peritoneum.

Fig. 9. Enlarged drawing of the portions *l* and *m* of Pl. 6, fig. 2. ($\times 270$). *a* cells corresponding to Pl. 6, fig. 2, *m* and filled with granules which stain with eosine, *b* corresponding to Pl. 6, fig. 2, *l* and filled with granules which stain with hematoxylin, *c* nuclei of the ciliated interstitial cells.

Fig. 10. Central nervous system and the semidiagrammatic longitudinal section of the buccal mass. ($\times 80$). *a* buccal mass and cavity, *b* odontophore with radula, *c* oesophagus, *d* cerebral ganglion with eye and otocyst, *e* pedal ganglion, *f* pleural ganglion, *g* buccal ganglion.

Fig. 11. Thin-walled anal organ. ($\times 270$). *a* granular contents, *b* lining cells with large nuclei, *c* peritoneum, *d* duct of anal organ.

Fig. 12. Longitudinal section through the reno-coelomic canal. ($\times 270$). *a* cavity of the renal heart, *b* strongly ciliated epithelium of the reno-coelomic canal, *c* haemocoele.

Fig. 13. Accessory renal gland. ($\times 270$). *a* composing gland cells, *b* peritoneum, *c* epithelium of the side branch of the ureter.

Fig. 14. Transverse section of the renal sac. ($\times 270$). *a* lining cells, *b* peritoneum, *c* haemocytes.

Fig. 15. Egg-band. ($\times 40$).

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PLATE 7

